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The Expanded Adaxial Epidermis of *Equisetum* Rhizome Sheath Teeth

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Plants of *Equisetum* have an extensive rhizome system that produces nodal buds that grow into either aerial stems or branches of the rhizome. Certain species also have tuber buds. Both the aerial stems and the rhizomes of *Equisetum* have nodal sheaths bearing a crown of teeth. The sheath is interpreted as a whorl of fused leaves, with the teeth representing the free tips of the individual leaves. The buds consist of a series of superposed sheaths that overarch the shoot apex. Subsequent intercalary meristematic activity at the base of each nodal sheath separates the nodal sheaths and produces the internodes.

The sheath teeth of the subterranean buds have a distinctive adaxial epidermis, a feature rarely noted in the literature. Francini (1942) compared rhizome and aerial buds of *E. ramosissimum*, and described trichomes developing from the inner epidermis of the rhizome sheath teeth and growing together to help the teeth form a cap protecting the apex. She also described mucilage production from the abaxial epidermis of the outer sheaths and pointed out how only one internode at a time elongates in the rhizome. Sachs (1882, p. 401) included a figure of a longitudinal section through an underground bud of *Equisetum arvense* showing an elaboration of the adaxial surface of the sheath teeth, but he did not describe this feature. Sadebeck (1902, p. 532) copied Sachs' figure, but did not mention the structure of the adaxial surface of the teeth. The purpose of this study is to describe more completely this little noted anatomical feature of *Equisetum*, and to speculate on its function.

MATERIALS AND METHODS

Rhizomes of *Equisetum hyemale* L., *E. arvense* L., and *E. telmateia* Ehrh. subsp. *braunii* (Milde) Hauke were excavated, washed, and their buds removed. Potted plants of *E.* ×*schaffneri* Milde, *E. scirpoides* Michx, and *E. diffusum* Don were depotted and rhizome terminal buds removed. The buds were killed and fixed in FAA for 24 hours and then stored in 70% EtOH. Sources of material are given on Table 1.

The outermost sheath was dissected from the bud. The clean bud was dehydrated in a tertiary butyl alcohol series, embedded in Paraplast (56–57°C), sectioned on a rotary microtome at 15 μm (longitudinal sections) or 20 μm (transverse sections), stained with safranin-fast green or safranin-toluidine blue (Berlyn & Miksche, 1976), and mounted in diaphane. Photos were taken on Kodak Plus-X film with a Nikon Microflex UFX camera mounted on a Zeiss microscope.

Buds used for scanning electron microscopy (SEM) were dehydrated in an ethanol series that included two changes of 100% ethanol and critical point dried

TABLE 1. Sources of Material of *Equisetum* Rhizome Buds.

Species	Locality	Voucher[1]
E. arvense	Rhode Island, Galilee	*Hauke 516*
E. arvense	Rhode Island, Kingston	*Hauke 514*
E. diffusum	Greenhouse, Univ. Rhode Island (originally from near Simla, India)	*Hauke s.n.*
E. hyemale var. *affine*	Rhode Island, Galilee	*Hauke 515*
E. ×schaffneri	Greenhouse, Univ. Rhode Island (originally from near San Jose, Costa Rica)	*Hauke 205*
E. scirpoides	Greenhouse, Univ. Rhode Island (originally from near Rutland, Vermont)	*Hauke 490*
E. telmateia subsp. *braunii*	California, Oakland, Claremont Canyon	*Hauke C1*

[1] All in KIRI.

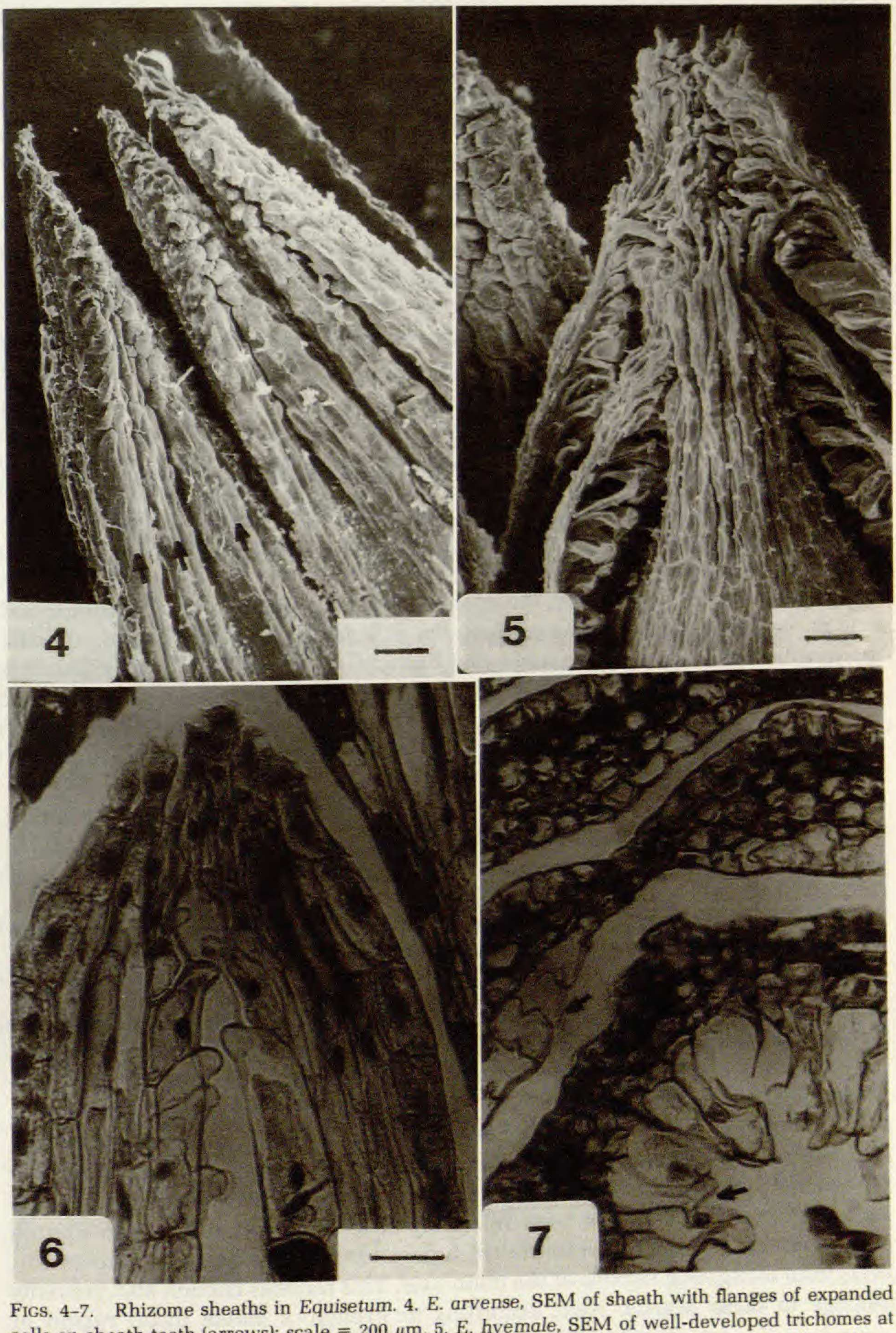
using CO_2 substitution and a Tousimis Samdri-PVT-3B critical point drier. They then were mounted on aluminum stubs with double-sided tape, coated with gold-palladium in a Hummer II coater, and observed with a Cambridge S4 scanning electron microscope.

RESULTS

The rhizome buds of *Equisetum* are different from the aerial stem buds in being sharply pointed (Fig. 1) and in having fewer, superimposed sheaths. Rather than the simultaneous development of several internodes, one internode elongates at a time. Roots develop at each node, but branches (rhizome or aerial) develop only occasionally. Numerous nodal buds are initiated, each with a root apical initial and a shoot apical initial. Frequently the root apical initial is functional, while the shoot apical initial generally is dormant or aborts. Occasionally the shoot apical initial becomes active, and the bud subsequently enlarges and erupts through the nodal sheath. Abundant mucilage, apparently produced by the abaxial epidermis, is associated with the rhizome buds, and is particularly obvious when the outermost sheath is dissected from the bud. Those buds destined to produce aerial shoots will possess these same features as they develop at the rhizome node, but change as they grow upward.

The sheath is initiated as a nodal ring, from the upper edge of which a crown of teeth is initiated, grows rapidly upward, and arches over the shoot apex. Then the nodal ring grows upward to produce a sheath consisting of a whorl of segments, one under each tooth, joined laterally by commissures (Hauke, 1985). The adaxial epidermis of the teeth of the rhizome sheath becomes greatly inflated as the teeth elongate and arch over to form a conical cap over the apex (Fig. 3). At first the apical ends of the outer walls of the epidermal cells expand and form papilliform trichomes (Fig. 2), while later the entire cell enlarges and a vertical flange is formed on the adaxial face of the rhizome sheath teeth (Fig. 4). Since the sheath teeth arch inward to form a convex cone the vertical flanges press together to fill the space above the next inner sheath.

FIGS. 1–3. Rhizome buds in *Equisetum*. 1. *E.* ×*schaffneri*. 2. *E. telmateia*, SEM of young sheaths with distinct papilliforme trichomes; scale = 50 μm. 3. *E. arvense*, longisection of bud with overarching sheaths showing expanded adaxial epidermis (arrows); scale = 50 μm.



FIGS. 4–7. Rhizome sheaths in *Equisetum*. 4. *E. arvense*, SEM of sheath with flanges of expanded cells on sheath teeth (arrows); scale = 200 μm. 5. *E. hyemale*, SEM of well-developed trichomes at apices of young sheaths; scale = 200 μm. 6. *E. scirpoides*, longisection of sheath apex with papillae; scale = 50 μm. 7. *E. arvense*, transsection of sheaths with expanded adaxial epidermis (arrows). Scale as in Fig. 6.

Differences exist in the degree of initial outgrowth of the apical end of the epidermal cells, so that in some species there is a more trichome-like appearance of the adaxial epidermis than in others. *Equisetum hyemale* (Fig. 5) shows the most trichome-like appearance of the adaxial epidermis, followed by *E.* ×*schaffneri*, *E. telmateia* (Fig. 2), *E. diffusum*, *E. arvense* (Fig. 3), and *E. scirpoides* (Fig. 6). In the last named species, the epidermal outgrowths are mere papillae. The initial apical expansion is most pronounced in the acropetal cells, and there is a transition in epidermal cell size from highly expanded to normal as one moves from apex to base of a sheath tooth in all species studied (Fig. 3). Thus, in a transverse section showing concentric sheaths, the outer sheaths show less epidermal inflation than the inner ones (Fig. 7). The earliest (i.e., outermost and subsequently lowermost) sheaths on buds destined to become aerial shoots also show rhizomatous features.

Discussion

My observations are consistent with Francini's (1942) description of the expanded inner epidermis of *Equisetum* rhizome sheath teeth. She described the sheath teeth as producing trichomes, which curve upward toward the center of the apex, intertwine, and fill the conical space. According to her, they begin to form in the second sheath from the apex (second youngest sheath), become quite long in the third, and interweave along the axis and develop thickened walls in the fourth sheath. At first I thought that Francini's description of the expanded epidermis was erroneous, because the whole epidermal cell appeared expanded, rather than having a trichome grow from it. The reason for the initial discrepancy between Francini's observations and mine then became obvious, because I could see that initially there was a distinct outgrowth from the upper end of the epidermal cell, followed by a more general expansion of the whole cell. To describe them as trichomes is somewhat misleading. The outgrowths in *E. scirpoides*, *E. arvense*, and *E. diffusum* are more accurately described as papillae, which Uphof (1962) defines as being unicellular, slightly elongated, and little differentiated. Since the structures in *E. telmateia*, *E.* ×*schaffneri*, *E. hyemale*, and probably *E. ramosissimum* are more elongated but still unicellular and little differentiated, they should be referred to as papilliform trichomes. The term "papillenhaare" of Eckhart, or papillate hair, is used for trichomes with a papillose surface (Uphof, 1962) and cannot be used in this case.

The sharply pointed bud ends, expansion of one internode at a time, mucilage production, and expanded adaxial epidermis of *Equisetum* rhizome buds probably all relate to the growth of rhizomes through the ground, and resultant forcing of the apical bud through the soil. The pointedness of the bud could help penetrate the soil. The expansion of one internode at a time would permit a node to complete its development and initiate roots relatively close to the growing point. French (1984) pointed out that the rhizomes of *Equisetum* delay outgrowth of roots and buds from elongating regions of the main axis. This reduces friction and prevents damage to these organs. Also, according to French, a single distal region of elongation better provides the force for soil penetration than would several active intercalary meristems separated by distances up to several centimeters in length.

The younger sheaths remain enclosed and protected by an older, more indurated sheath for a longer time. The mucilage possibly facilitates the passage of the apical bud through both the oldest enclosing sheath and the soil. The mucilage may also protect the tissues from soil microorganisms. Finally, the expanded adaxial epidermis may, by filling the conical space formed by the enclosing teeth, maintain the sharply pointed form of the sheath as it pushes through the soil, then yield to the next sheath pushing through it.

The rhizome has an apical meristem protected by young leaves. The growing rhizome, subjected to stresses similar to those of a growing root, requires a structure analagous to the root cap for protection against these stresses. In the case of *Equisetum*, the shoot apical bud of a rhizome functions in a similar manner to a root apex. To prevent their being injured by elongation of the root, root hairs do not develop until elongation ceases. Similarly, *Equisetum* nodal roots develop after elongation of the internode below them ceases, and elongation of one internode at a time permits this to occur close to the apex. Mucilage is associated with root apices, and *Equisetum* rhizome buds produce copious mucilage. The root apex forms a root cap, which is continually parting the soil to permit the apex to penetrate, and is continually being replaced by the apex. Similarly, *Equisetum* rhizome apices have a cap of superposed sheaths. These sheaths are sharply pointed to penetrate the soil, are strengthened by the expanded adaxial epidermis, and are continually being grown through by the apex, as well as continually being replaced. Thus the expansion of the adaxial epidermis of the rhizome sheath teeth of *Equisetum* is probably part of the structural adaptation that permits the rhizome to grow successfully in the soil.

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